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PREDATOR-PREY INTERACTIONS BETWEEN EAGLES AND CACKLING CANADA AND ROSS' GEESE DURING WINTER IN CALIFORNIA

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Abstract.—Cackling Geese (*Branta canadensis minima*) were preyed on heavily in northeastern California by Golden Eagles (*Aquila chrysaetos*) and less commonly by Bald Eagles (*Haliaeetus leucocephalus*) in 1985–1990. Eagle predation on Cackling Geese was minimal in other wintering locations in California. In the Klamath Basin, eagles killed Cackling Geese most frequently soon (<10 days) after the geese arrived in the fall. Eagles killed fewer Cackling Geese in the Klamath Basin when Cackling Geese were less common than Ross' Geese (*Chen rossii*) and Lesser Snow Geese (*C. caerulescens caerulescens*). We also examined spatial and temporal (daily, seasonal, and annual) variation in eagle predation on geese at a smaller scale in Big Valley, California. Most eagle-caused flushes of geese occurred during mid-day when the geese were using traditional day-roost sites. Roosting on water with most other Cackling and Ross' Geese in Big Valley reduced the frequency of eagle attacks relative to other sites. In Big Valley, the larger Great Basin Canada Goose (*Branta canadensis moffitti*) was attacked by Golden Eagles only once during 88 observation days, while the smaller Cackling and Ross' geese were attacked by Golden Eagles a total of 27 times. Moreover, Cackling Geese in Big Valley were attacked and killed at least twice as often as Ross' Geese because Cackling Geese often grazed in pasture where Golden Eagle attacks were more frequent. When feeding on pasture, geese did not increase time spent vigilant or flock size compared to habitats with less eagle predation. The antipredator behavior of Cackling Geese includes maintaining high levels of vigilance, occurring in large, dense flocks, and roosting on water during nonfeeding periods. When attacked by eagles, Cackling Geese used socially-coordinated and speed-based escape tactics. *Received 2 June 1993, accepted 15 Sept. 1993.*

An individual bird may join a flock to reduce the chance of being attacked or of being caught when attacked (see Bertram 1978). Birds in flocks may be safer than solitary individuals for at least three reasons. Individuals in a group may detect predators better or earlier than smaller groups or solitary individuals (Pulliam 1973, Siegfried and Underhill 1975, Kenward 1978, Lazarus 1979). A predator which attacks a group of prey may become confused and catch fewer prey (Neill and Cullen 1974, Milinski 1979, Landeau and Terborgh 1986). Finally, an individual in a group may reduce its chance of being caught simply because of a dilution-effect (Foster and Treherne 1981).

Flocking creates a tradeoff between avoiding predators and feeding efficiently (Powell 1974, Caraco 1979a, b, Caraco et al. 1980, Pulliam

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and Caraco 1984, Poysa 1987). Individuals in larger groups generally enjoy greater protection from predators, but as groups become larger the antipredator benefits may diminish and costs associated with, for example, foraging and social dominance may increase (reviewed by Curio 1976, Pulliam and Caraco 1984, Black 1988, Elgar 1989).

We investigated the predator/prey relationship between eagles and Cackling Geese (*Branta canadensis minima*), Great Basin Canada (*B. canadensis moffitti*), and Ross' (*Chen rossii*) Geese on wintering areas in California. Golden (*Aquila chrysaetos*), and particularly Bald Eagles (*Haliaeetus leucocephalus*), congregate in many of the same areas as waterfowl during winter in northeastern California, making interactions between eagles and geese frequent and observable. We measured variation in the frequency of eagle predation on Cackling Geese at two spatial scales (geographic and local) and three temporal scales (annual, seasonal, and daily). We evaluated some causal mechanisms for this variation in predation risk. We then explored whether Cackling Geese modify their flock size or time spent vigilant in response to variation in the risk of eagle predation.

Although direct predation on adults has minor impacts on population dynamics of geese (reviewed by Owen 1980), predators may strongly influence avian systems through effects on behavior and distribution of birds rather than through direct mortality (reviewed by Lima and Dill 1990, Lima 1993). Cackling Geese are among the smallest geese in North America, averaging about 1.5 kg in winter (Raveling 1978). Their small body size may lead to increased predation risk and account for some of their unique social organization (Johnson and Raveling 1988, Owen and Black 1990, McWilliams and Raveling, in press). Where Cackling and Ross' Geese form mixed species flocks in northeastern California, they often occur sympatrically with the larger Great Basin Canada Goose. In this paper, we compare the frequency of eagle predation on sympatric Great Basin, Cackling, and Ross' geese in Big Valley, California. Such interspecific comparisons reveal how differences in body size of geese influences risk of eagle predation which then may influence goose social behavior.

METHODS

An intensive study of the numbers, distribution, and annual survival of neck-banded Cackling Geese was conducted during winter, 1982–1983 through 1987–1988 (Raveling et al. 1992). Before fall 1985, observations of eagle activity were not consistently recorded. Three observers in 1985–1986 and two observers in 1986–1987 observed Cackling Geese from dawn until dusk almost daily between mid-October through late-April. In 1987–1988, we spent fewer days observing geese, and we concentrated our effort primarily in Klamath Basin, Sacramento Valley, and San Joaquin Valley (Fig. 1).

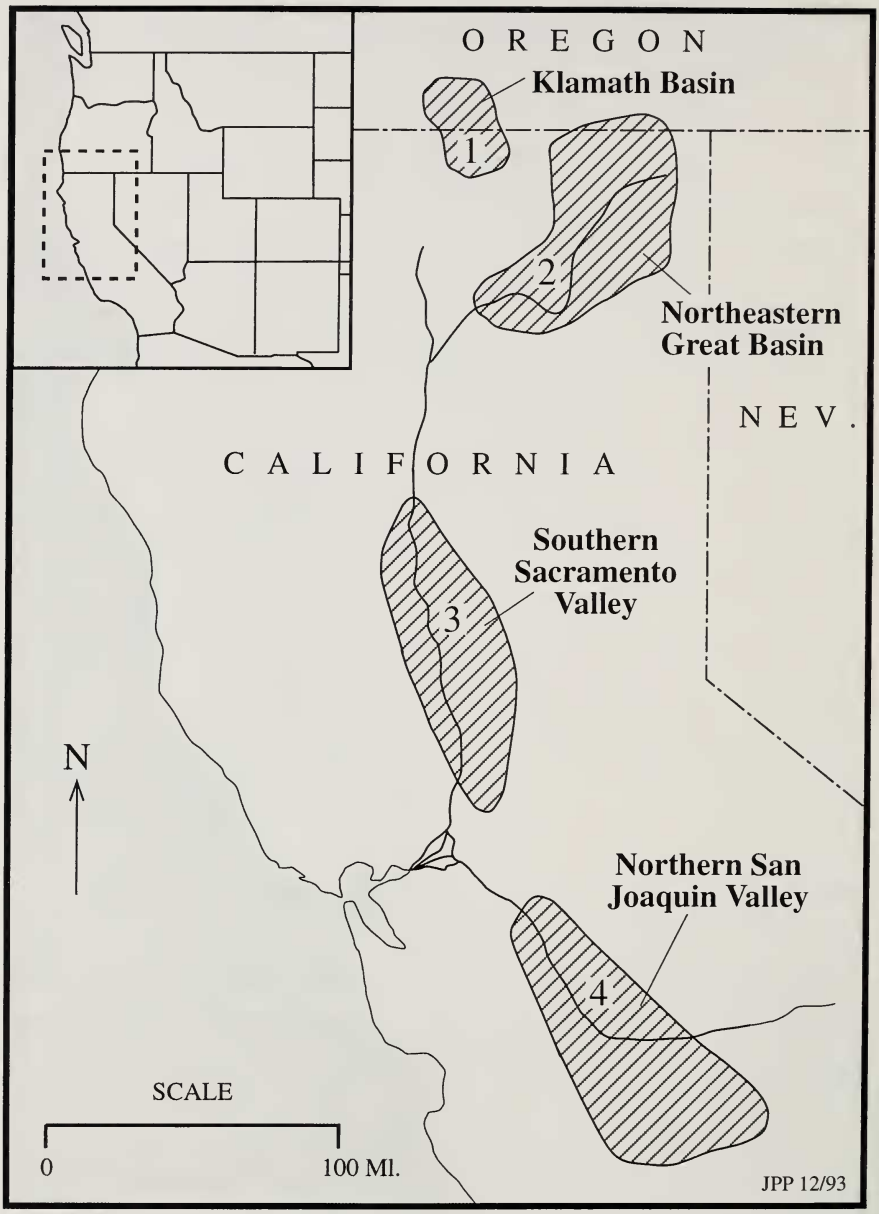

FIG. 1. Geographic locations in California used by Cackling Geese during the nonbreeding season. Specific locations in each area where most observation effort was concentrated are Tulelake National Wildlife Refuges (NWR) (1), Big Valley (2), Sacramento Valley NWRs (3), and Merced NWR (4).

We included a day in the analysis only when we had observed geese for >8 h. Observation effort in any one location in California was dictated primarily by movements of the geese (Johnson 1988, Raveling et al. 1992). During our study, Cackling Geese used the Klamath Basin (Fig. 1) between mid-October and early-December. Between early-December and mid-January, most Cackling Geese in California were found in the Sacramento and San Joaquin valleys. After mid-January and before their departure in late-April for Alaska, Cackling Geese moved to the San Joaquin Valley, Big Valley, or Klamath Basin. Thus, comparisons of these four locations in California includes a seasonal component.

Two observers in 1989 and three observers in 1990 observed Cackling and Ross' geese in Big Valley on a daily basis between 1 March and their respective departures in mid- and late-April. An observation day was included in the analysis only if geese were followed from dawn until dusk. When a goose flock flushed, we recorded the probable cause of the flush. We assumed an eagle caused the flush if we observed an eagle flying in the area and if the direction of the initial flush was away from the direction of the eagle. We recorded the date, time, and location of all eagle-associated flushes, attacks, and kills. An eagle attack was designated only when an eagle stooped and/or chased geese. In addition, whenever a goose flock was flushed by an eagle we estimated the size and species composition of the flock.

California Dept. of Fish and Game (CDFG) biologists coordinated counts of Bald Eagles throughout California during mid-January 1979–1981 and from 1986 to the present (Detrich, unpubl. data; Nahstoll, unpubl. data). We used these counts to estimate general distribution and population trends of Bald Eagles during our study. We used counts of Golden Eagles recorded during the mid-January Bald Eagle survey as an indication of the relative occurrence of Golden Eagles in specific geographic locations in California.

Because geese concentrated in and around refuges, we also used eagle population estimates made by biologists at Sacramento National Wildlife Refuges (specifically Sacramento, Delevan, and Colusa NWR) and at Klamath Basin National Wildlife Refuges (specifically Lower Klamath and Tulelake NWR). Biologists at both refuge complexes conduct bimonthly surveys of all waterfowl species and eagles. In addition, raptors at Tulelake and Lower Klamath NWR are censused bimonthly from 1 October–30 April along a series of transects established in 1985. In the results, we specify whether we are using the mid-January counts, bimonthly surveys, or bimonthly transect counts to estimate eagle numbers, or the proportion of Bald/Golden eagles in the population.

We used *G*-tests (Sokal and Rohlf 1981) for testing hypotheses about frequencies of eagle attacks and flushes in Big Valley in different habitats and across the daily period. The expected frequency distribution for testing habitat-related patterns in eagle attacks and flushes was determined by dividing the area of each goose habitat type by the total area used by the geese. These proportions are: day roost (0.046), pasture (0.597), alfalfa (0.139), wet meadow (0.140), and winter wheat (0.078). The expected frequency distribution for testing daily patterns in eagle attacks and flushes was determined by dividing the duration of each of the three time periods by the total time spent watching geese per day. These proportions are: morning (0.286), mid-day (0.428), and evening (0.286).

In 1989, we watched geese for similar amounts of time on all habitats except for winter wheat (day roost/wet meadow = 116 h, pasture = 113 h, alfalfa = 108 h, winter wheat = 32 h). In 1990, we spent more time watching geese on wet meadow and alfalfa (day roost/wet meadow = 270 h, pasture = 114 h, alfalfa = 194 h, winter wheat = 42 h). Consequently, prior to statistical analysis, we expressed all habitat-related patterns in eagle attacks and flushes per 100 hours of observation basis. Whenever expected values for one of the two years was less than 10, we pooled frequencies for both years.

We compared sizes of goose flocks flushed by eagles on four feeding habitats and the

TABLE 1

FREQUENCY OF EAGLES KILLING CACKLING GEESE AND MID-JANUARY POPULATION ESTIMATES OF BALD EAGLES AT SELECTED WINTERING LOCATIONS IN CALIFORNIA

Location and year	No. obs. days	Golden Eagle		Bald Eagle		No. Bald Eagles in mid-Jan.
		Kills	Predation rate[a]	Kills	Predation rate[a]	
Klamath Basin						
Oct.–Dec. 1985	47	2	1.3	1	0.6	109
Oct.–Dec. 1986	78	6	2.3	2	0.8	130
Oct.–Dec. 1987	30	10	10.0	0	—	965
Sacramento Valley						
Nov. 1985–March 1986	58	0	—	0	—	No count[b]
Nov. 1986–March 1987	51	1	0.6	0	—	9
Nov. 1987–March 1988	23	0	—	0	—	4
San Joaquin Valley						
Feb.–April 1986	42	0	—	0	—	Poor count[b]
Feb.–April 1987	35	1	0.9	0	—	3
Feb.–April 1988	11	0	—	0	—	3
Big Valley						
March–April 1989	38	2	1.6	0	—	7
March–April 1990	50	3	1.8	0	—	6

[a] No. of eagle kills observed divided by number of observation days × 30 days.
[b] Caused by extensive fog during count period.

day roost in Big Valley for 1989 and 1990 using an unbalanced design analysis of variance (ANOVA) (Sokal and Rohlf 1981). If we observed a flock of geese flushed more than once by eagles at the same location on the same day, we used the average flock size for that day in the analysis. The flock size data conformed to the assumptions of ANOVA.

RESULTS

Large-scale spatial and temporal variation in eagle predation.—Eagles were observed killing Cackling Geese on average once every three days in the Klamath Basin, but the frequency of eagle kills varied annually (Table 1). Only one eagle kill was seen in 132 observation days in Sacramento Valley and 88 observation days in the San Joaquin Valley. In Big Valley, eagles were observed killing Cackling Geese every 17–19 days on average. Golden Eagles were responsible for 89.3% of all Cackling Goose kills observed. Bald Eagles were observed killing Cackling Geese only in the Klamath Basin where they were responsible for 14% of all eagle kills observed. We observed an immature eagle attacking and killing a Cackling Goose only once.

The Klamath Basin contained over 10 times more Bald Eagles, in any

given year, than the other three locations where Cackling Geese congregated (Table 1). Golden Eagles in northeastern California represented 26–51% of the total number of Golden Eagles observed in California during the mid-January surveys in 1979–1981, whereas the Central Valley of California (including Sacramento and San Joaquin valleys) contained only 9–11% of all Golden Eagles observed (Detrich, unpubl. data). Unfortunately, few observations of Golden Eagles have been reported during the mid-January surveys since 1981. Big Valley had 6–7 Bald Eagles (Table 1) and probably 3–4 Golden Eagles (McWilliams, pers. obs.) in 1989 and 1990, making it second only to the Klamath Basin in eagle population density.

Annual changes in Bald Eagle populations were most evident in the Klamath Basin (Table 1), where nearly 1000 wintering eagles were observed in 1987. Despite this large concentration of Bald Eagles, more geese were killed by Golden Eagles than by Bald Eagles in 1987 (Table 1). Based on the raptor transect counts at Tulelake NWR, 1.5%, 3.0%, and 0.8% of eagles were identified as Golden Eagles in 1985, 1986, and 1987, respectively. Applying these percentages to the bimonthly aerial counts of eagles at Tulelake NWR, we estimated between one and eight Golden Eagles were present each fall, 1985–1987.

We observed eagles killing Cackling Geese within two days of their arrival in the Klamath Basin and at least one month prior to peak eagle populations (Fig. 2). During fall 1985, we saw three Cackling Geese killed by eagles. All three geese were killed soon after most Cackling Geese had arrived in the Klamath Basin and when Cackling Geese were most abundant. During fall 1986, we saw six Cackling Geese killed by eagles. Five of the six geese were killed during the approximately 25-day period when Cackling Geese were arriving in the Klamath Basin and when they were most abundant. During fall 1987, eagles killed 10 Cackling Geese in 10 days. During these 10 days, most Cackling Geese arrived in the Klamath Basin and peak counts of Cackling Geese were recorded.

The pattern of eagle predation on Cackling Geese was also related to the availability of alternative prey. During fall 1985, we saw no Cackling Geese killed by eagles after white geese arrived in the Klamath Basin. After white geese arrived in the Klamath Basin in fall 1986, we observed only one eagle kill a Cackling Goose even though Cackling Goose abundance remained relatively high during November and December (Fig. 2). During fall 1987, there were more Cackling Geese than in 1985 and 1986 and white geese never were abundant. We observed more Cackling Geese killed by eagles in fall 1987 than in fall 1985 and 1986.

Geese crippled or killed by hunters may provide more susceptible prey for eagles and thus reduce eagle attacks on healthy geese. If carrion avail-

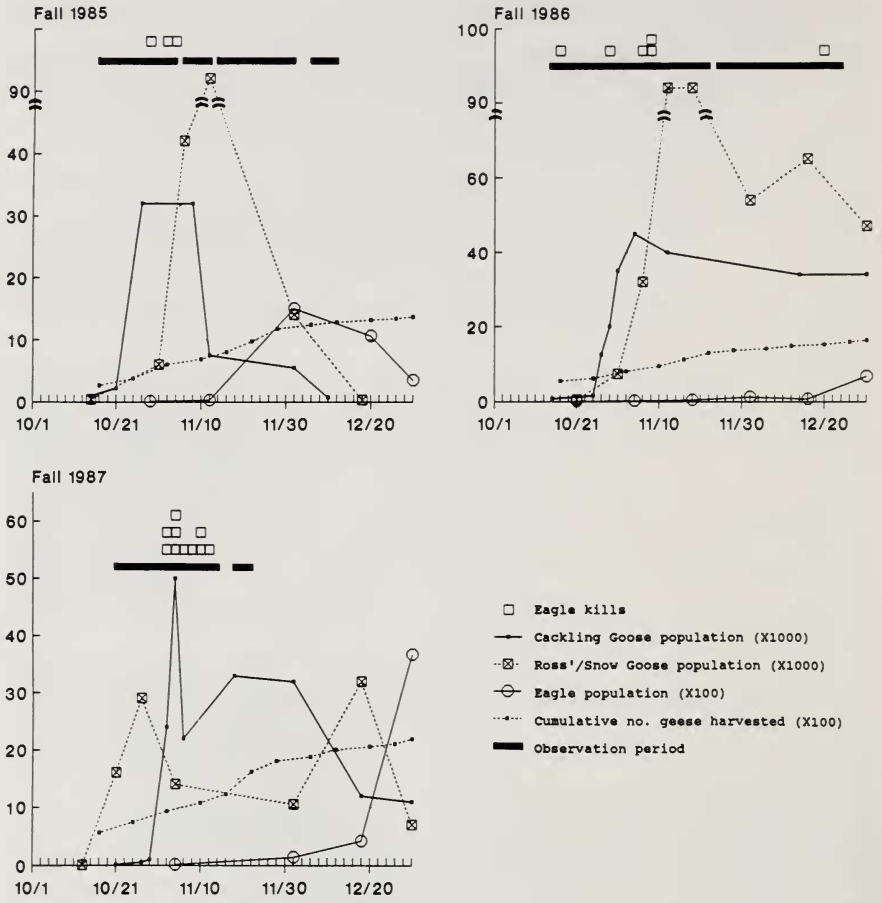

FIG. 2. Possible factors which influence the temporal pattern of eagles killing Cackling Geese during fall, 1985–1987, at Tulelake NWR, CA. Cackling Goose population estimates are based on our counts. White geese (Ross' and Lesser Snow geese) and eagles were counted during bimonthly aerial censuses conducted by Tulelake NWR personnel. Goose harvest data was also collected by Tulelake NWR personnel. Observation period includes all days when at least eight hours per day were spent observing geese.

able to eagles is directly proportional to the number of geese shot by hunters, then almost twice as many geese were available as carrion in 1987 compared to 1985 and 1986 (Fig. 2). In 1987, we saw no Bald Eagles kill a Cackling Goose, while Golden Eagles preyed heavily on Cackling Geese (Table 1).

Spatial and temporal changes in eagle predation in Big Valley.—In both 1989 and 1990, the rate of eagle-caused flushes in Big Valley was

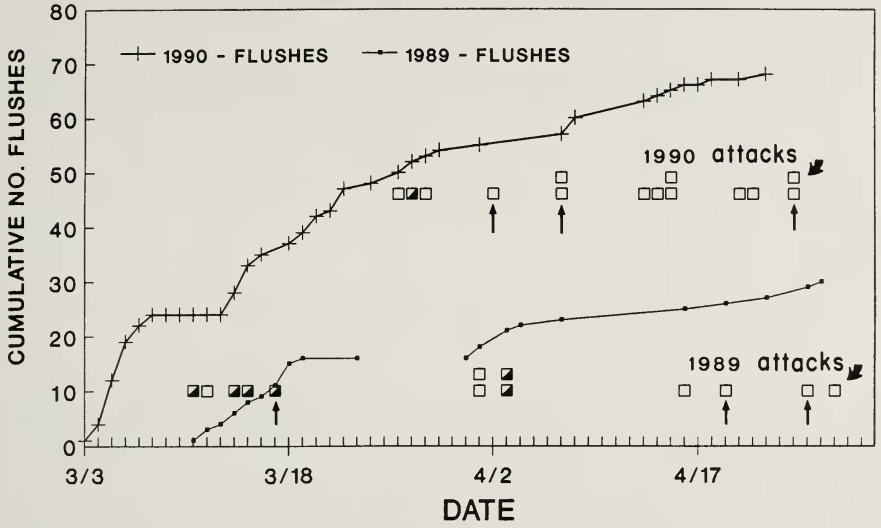

FIG. 3. Temporal patterns of eagle-caused flushes, eagle attacks, and eagle kills of geese in Big Valley, California during March and April, 1989 and 1990. Unshaded squares denote days eagles attacked Cackling Goose flocks. Half-shaded squares denote days eagles attacked mixed Ross'/Cackling goose flocks. Arrows denote attacks which resulted in a goose being captured by the eagle.

highest just after arrival of the geese (2.1 flushes/day between 11–19 March in 1989, 5.0 flushes/day between 3–7 March in 1990), and then declined to 0.4 flushes/day between 3–25 April in 1989 and 0.7 flushes/day between 25 March–24 April in 1990 (Fig. 3). The rate of eagle-caused flushes was consistently higher in 1990 than in 1989. In 1989, 36% of eagle attacks occurred during the time when the rate of eagle-caused flushes was highest. In 1990, all eagle attacks occurred during the period when eagle flush activity was at its lowest rate.

In 1989 and 1990, we observed 62% and 43%, respectively, of eagle-caused flushes during mid-day (Table 2). Eagle attacks in 1989 occurred primarily during mid-day or evening periods, whereas in 1990 most eagle attacks occurred during the evening period. When differences in the amount of observation time for each time-of-day period were considered for both years, the frequency of eagle flushes did not vary across the daily period ($G = 1.75$, $P > 0.05$), but the frequency of attacks was higher in the evening ($G = 8.62$, $P < 0.05$).

More eagle-caused flushes occurred on day roost site(s) than expected (Table 3, total for both years), based on its proportion of the total area ($G = 116.8$, $P < 0.01$). However, frequency of eagle attacks on the day

TABLE 2

FREQUENCY WITH WHICH CACKLING AND ROSS' GEESE WERE FLUSHED, ATTACKED, AND KILLED BY EAGLES DURING THREE DAYTIME PERIODS IN BIG VALLEY, CALIFORNIA

Time-of-day[a]	1989			1990			Total		
	Flushes	Attacks	Kills	Flushes	Attacks	Kills	Flushes	Attacks	Kills
Morning	4	2	0	22	3	0	26	5	0
Mid-day	20	6	2	30	1	1	50	7	3
Evening	8	5	1	18	10	2	26	15	3

[a] Morning = 06:00–10:00 PST, Mid-day = 10:00–16:00 PST, Evening = 16:00–22:00 PST.

roost or on any feeding site was not different than expected ($G = 7.31$, $P > 0.05$). Geese typically used the day roost between 10:00–16:00 h PST, spending most of this time resting on the water or shore. However, portions of the mid-day period were usually spent feeding in wet meadows adjacent to the day roost. When the relative sizes of habitats used by feeding geese were considered, comparisons of only feeding sites revealed differences in eagle-caused flushes ($G = 26.7$, $P < 0.01$) but no differences in eagle attacks ($G = 0.78$, $P > 0.05$). Five of the six geese killed by eagles occurred while geese were feeding on either pasture or wet meadow sites.

If expected values were calculated assuming equal likelihood of attacks or flushes in each feeding habitat, the frequency of flushes was higher in pasture and wet meadow ($G = 8.99$, $P < 0.05$) and the frequency of attacks was higher in pasture ($G = 9.35$, $P < 0.05$) compared to other habitats where geese fed.

Predation pressure differences for sympatric geese.—In 1989 and 1990, we observed seven and 13 eagle attacks, respectively, on pure

TABLE 3

FREQUENCY WITH WHICH CACKLING AND ROSS' GEESE WERE FLUSHED, ATTACKED, AND KILLED BY EAGLES WHILE ON THE DAY ROOST OR ON SPECIFIC FORAGING HABITATS IN BIG VALLEY, CALIFORNIA

Habitat	1989			1990			Total		
	Flushes	Attacks	Kills	Flushes	Attacks	Kills	Flushes	Attacks	Kills
Day roost	14	4	1	46	2	0	60	6	1
Wet meadow	4	1	1	8	3	2	12	4	3
Pasture	10	6	1	6	6	1	16	12	2
Alfalfa	1	1	0	6	3	0	7	4	0
Winter wheat	3	1	0	2	0	0	5	1	0

TABLE 4

FREQUENCY OF GOLDEN EAGLE ATTACKS AND KILLS FOR CACKLING, ROSS', AND GREAT BASIN CANADA GEESE IN BIG VALLEY, CALIFORNIA

Goose species	1989			1990		
	Attacks	Kills	Predation rate	Attacks	Kills	Predation rate
Cackling	7	2	10.3[a]	13	3	8.4[b]
Ross'	0	0	5.3[c]	0	0	0.8[d]
Cackling and Ross'[e]	6	1	—	1	0	—
Great Basin	1	0	0.8[f]	0	0	0

[a] (13 attacks/38 obs. days) × 30 days.
[b] (14 attacks/50 obs. days) × 30 days.
[c] (6 attacks/34 obs. days) × 30 days; all attacks were on mixed flocks.
[d] (1 attack/40 obs. days) × 30 days; all attacks were on mixed flocks.
[e] Mixed species flocks.
[f] (1 attack/38 obs. days) × 30 days.

Cackling Goose flocks and no eagle attacks on the relatively rare pure Ross' Goose flocks (Table 4). Of the 20 observed eagle attacks on pure Cackling Goose flocks, 20% resulted in a Cackling Goose being caught and killed by an eagle. Of the seven observed eagle attacks on mixed Ross' and Cackling Goose flocks, only one Ross' Goose was killed. Eagles attacked mixed species flocks as often as pure Cackling Goose flocks in 1989 (6 of 13 attacks) but usually attacked pure Cackling Goose flocks in 1990 (13 of 14 attacks).

Cackling Geese were attacked by eagles an average of once every 3–4 days whereas Ross' Geese were attacked by eagles an average of once every 6–40 days (Table 4). We observed only one Golden Eagle attack on a Great Basin Canada Goose (Table 4).

Risk of eagle predation and the responses of geese.—In Big Valley, eagles attacked goose flocks of many sizes (Fig. 4). Flocks larger than 3000 geese were frequently flushed by eagles, but were less commonly attacked than smaller flocks. Eagles flushed larger flocks of geese on the roost site than on the four feeding habitats (Table 5; $F_{4,73} = 9.22$, $P = 0.0001$). In both 1989 and 1990, the predation risk experienced by an individual goose on a given habitat was highest when it was in a pasture (Table 5). Feeding geese typically spent 15–35% of the time with their heads up scanning for predators. Time spent vigilant was not significantly different across habitats (McWilliams and Raveling 1994).

Cackling and Ross' geese always responded to eagle attacks by flushing into the air. If geese were on water prior to the attack, they often circled in tight, compact flock(s) 30–200 m above the water. If the eagle persisted, the flock would usually become divided and the geese would try

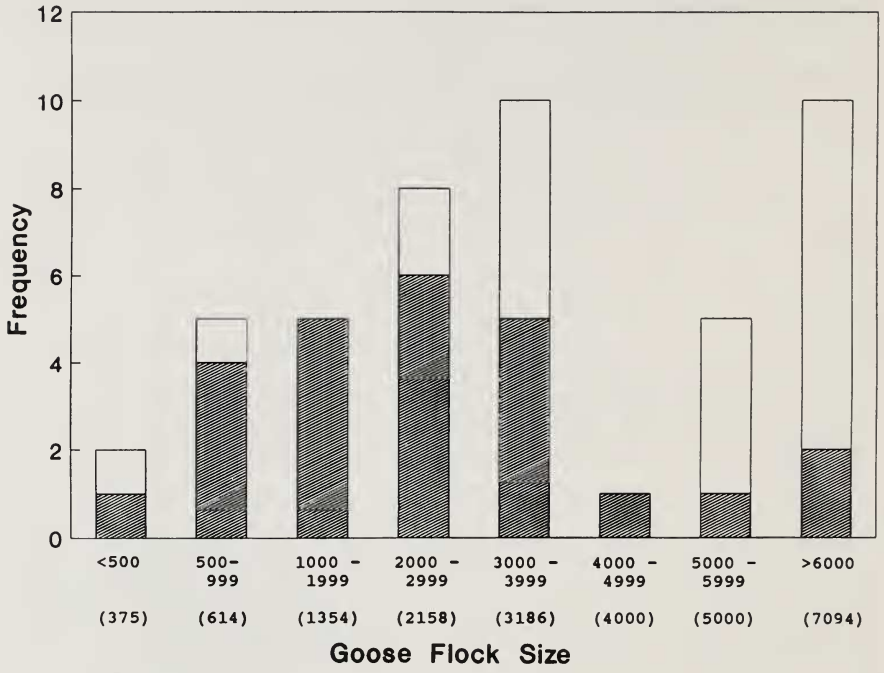

FIG. 4. Frequency distribution of goose flock sizes that were flushed or attacked by Golden Eagles in 1989 and 1990. One entire bar represents the number of flushes observed for a given flock size, and the hatched portion of each bar shows the number of flushes which escalated into attacks. Numbers in parentheses are the average flock size for each flock size class.

to outdistance the eagle by flying off as quickly as possible. While Cackling and Ross' Geese were flying about, Great Basin Canada Geese on the same field usually remained on the ground. The only eagle attack on a Great Basin Canada Goose that we observed involved a Golden Eagle grabbing the back of the goose. The goose then grabbed the eagle with its bill and hit the eagle with its wings. The eagle left within five min of initiating the attack and the goose suffered no apparent lasting effects.

DISCUSSION

Eagle/goose interactions at large and small spatial scales.—In general, geographic variation in the frequency of eagle predation on geese is best explained by patterns of eagle abundance. Of the 28 Cackling Geese we observed killed by eagles during 1985–1990, 93% were observed in northeastern California (including both Klamath Basin and Big Valley). Currently, the Klamath Basin supports the largest concentration of win-

TABLE 5

COMPARISON OF TIME SPENT VIGILANT, AVERAGE FLOCK SIZE, AND PREDATION RISK FOR CACKLING AND ROSS' GEESE AT THE DAY ROOST AND IN FOUR HABITATS COMMONLY USED WHILE FEEDING IN BIG VALLEY, CALIFORNIA

	Percent time vigilant[a]				Flock sizes flushed by eagles						Predation risk[b]	
	1989		1990		1989			1990				
Habitat	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	N	$\bar{x}$	SE	NE	1989	1990
Day roost	—	—	—	—	5536	680	14	4360	381	30[c]	7.2	4.6
Wet meadow	33	11	26	12	4625	375	4	2007	267	7[c]	2.2	14.9
Pasture	27	15	27	11	2125	555	10	1783	322	6	28.2	33.7
Alfalfa	26	14	16	10	1600	—	1	1933	81	6	6.3	15.5
Winter wheat	18	9	15	8	3467	1533	3	750	250	2	8.7	—

[a] Calculated from McWilliams and Raveling (1994); vigilance = % time with head above horizontal plane of back.

[b] Predation risk = (no. eagle attacks/mean flock size) × 10,000. Mean flock sizes used are those given above. Frequency of eagle attacks per habitat is from Table 3.

[c] Samples sizes are different than those in Table 3 because we did not always estimate goose flock size during an eagle attack or because, prior to ANOVA analysis, we averaged flock sizes flushed by eagles at the same location on the same day.

tering Bald Eagles in the contiguous U.S. (Palmer 1988a), along with impressive concentrations of over one million waterfowl (Keister et al. 1987). In some years, Golden Eagles are also more abundant in northeastern California than at other locations used by Cackling Geese, although population estimates for Golden Eagles in California are lacking. There is no evidence that geese respond to this large scale variation in eagle activity. Johnson (1988) found no significant differences in time-activity budgets of Cackling Geese in Klamath Basin, Sacramento or San Joaquin valley, or Big Valley during winter 1982–1983 and 1983–1984.

Once flocks of geese have at least 200 individuals, the time spent vigilant by individuals no longer decreases (Lazarus 1978, Inglis and Lazarus 1981). This may explain why Cackling Geese in Big Valley were not more vigilant in habitats with higher risk of predation. Small birds which live in small flocks (<20 birds) respond to increased predation risk by increasing group size (Caraco et al. 1980). In contrast, we found that although geese encountered spatial variation in predation risk, geese remained in flocks of about 2000 individuals across habitats. We suspect that flock size of Cackling and Ross' geese is dictated primarily by the distribution and abundance of food plants and by the local population size of geese, with some minimum flock size threshold determined by risk of predation. The fact that flock sizes were largest on the day roost where feeding does not occur suggests that some constraint(s) associated with feeding limits flock size in Cackling and Ross' geese.

Eagle/goose interactions at large and small temporal scales.—In the Klamath Basin, Cackling Geese were attacked by eagles more often in years when populations of Cackling Geese were large and when Cackling Geese stayed longer. Moreover, eagles reduced their hunting of Cackling Geese when white geese were more abundant than Cackling geese. These predation patterns suggest that Golden and Bald eagles feed disproportionately on the most abundant prey and that changes in the availability of alternative preferred prey influenced the pattern of eagle predation (also see Steenhof and Kochert 1988). The lack of a relationship between Bald Eagle population and frequency of eagles killing Cackling Geese is not surprising because the large concentrations of wintering Bald Eagles in the Klamath Basin feed primarily on scavenged waterfowl (Frenzel and Anthony 1989).

Eagles killed Cackling Geese most frequently 1–10 days after Cackling Geese arrived in the Klamath Basin each year. In Big Valley, we also observed more eagle/goose interactions soon after arrival of the geese. Geese may be more vulnerable to eagle predation on or after long migrations because of exhaustion (Ogilvie 1978:177), because they must spend more time eating to meet nutrient demands (Sedinger and Bollinger 1987, Raveling and Zezulak 1991) and are consequently less vigilant, or perhaps because they must learn that particular locations are more risky.

At all wintering locations in California, Cackling and Ross' geese traditionally spend the mid-day period on water at a roost site. When geese were on the day-roost in Big Valley, they experienced significantly more eagle-caused flushes but similar frequencies of attacks compared to habitats where geese fed. It appears the large mid-day concentration of roosting geese effectively reduced eagle predation attempts.

Nature of eagle/goose predator-prey relations.—Reports of Bald Eagles capturing birds as large as geese in flight are rare (e.g., Rudebeck 1950, 1951; Bennett and Klaas 1986; Nero 1987; Bartley 1988) and reports for Golden Eagles rarer still (see Palmer 1988b). Eagles adopt a variety of strategies when hunting geese, with ground attacks and stoops (Stalmaster 1987, Palmer 1988a, b) being the most common methods employed. All successful attacks we observed involved the eagle grabbing the back of the goose and then gliding to the ground. This type of capture is unlike that described by Brewster (1880), Herrick (1934), and Stalmaster (1987) in which the Bald Eagle grabbed the belly of the goose as the eagle performed a somersault maneuver. An element of surprise is a common feature of the eagle's hunting methods. The primary antipredator strategy of geese includes aggregation and early detection through vigilance combined with aerial escape. Cackling and Ross' geese used so-

cially-coordinated and speed-based tactics during aerial escape (after Lima 1993).

Body size differences between Great Basin Canada and Cackling geese strongly influenced the frequency of predation by eagles. Snow Geese, an intermediate-sized goose, are preyed on by eagles only rarely (Rudebeck 1950, 1951; Bennett and Klaas 1986; Nero 1987; Bartley 1988). The various species and subspecies of geese form a continuum of body sizes that includes the size threshold above which eagles apparently prefer not to attack. Probably in response to increased predation risk, the smaller body-sized geese occur in denser flocks and consequently have reduced family cohesiveness (Johnson and Raveling 1988). Whether predation alone is responsible for the evolution of this behavior is unlikely, because flocking in geese may also have important feeding advantages (Owen and Black 1990).

Ross' and Cackling geese are similar in size, but Cackling Geese were attacked and killed at least twice as often as Ross' Geese in Big Valley. We suggest this interspecific difference in frequency of predation occurs primarily because Cackling and Ross' geese have different foraging strategies. Both Cackling and Ross' geese graze in similar habitats, but the two species differ in the proportion of time spent on specific habitat types (McWilliams and Raveling, in press). Cackling Geese spent 16–52% ($\bar{x}$ = 34%) of their foraging time during March and April on pasture where eagles are more active, whereas Ross' Geese spent 0–15% ($\bar{x}$ = 4%) of their foraging time on pasture.

An alternative explanation for the higher rate of predation on Cackling Geese is that eagles simply prefer Cackling Geese and consequently follow them to their feeding sites. We believe this is less likely because, compared to other sites where geese fed in Big Valley, pasture areas had more Belding and California ground squirrels (*Citellus beldingi* and *Otospermophilus beecheyi*) and black-tailed jackrabbits (*Lepus californicus*) which are the most frequent prey of Golden Eagles in northeastern California (Bloom and Hawks 1982).

Predator-prey systems, like the eagle-goose system we have analyzed, are probably often strongly influenced by the predatory behavior of individuals (Rudebeck 1950, 1951; Page and Whitaker 1975; Palmer 1988a, b). All six successful eagle attacks on geese that we observed in Big Valley were made by a single adult male Golden Eagle identifiable by a white wing patch (see Jollie 1947:572). This one eagle was not responsible for the majority of eagle-caused flushes, but was responsible for the majority of eagle attacks on goose flocks.

In summary, we found that spatial and temporal variation in eagle predation on Cackling Geese was related to variation in the abundance

and distribution of eagles, geese, and alternative prey. Geese did not modify their vigilance time or flock size in response to spatial and temporal variation in predation risk. Interspecific differences in the susceptibility of geese to eagle attacks were strongly influenced by the body size and foraging strategy of the geese. Cackling Geese reduced the risk of eagle predation by occurring in large, dense flocks, detecting eagles through vigilance, and by resting with many other geese in locations which provided some protection from eagles.

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